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FOSSIL SCOLEBYTHIDS (HYMENOPTERA: SCOLEBYTHIDAE) FROM LEBANESE AND DOMINICAN AMBER

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Abstract.—The first two fossil species of Scolebythidae are described: **Libanobythus milkii,** n. gen., n. sp., from Lebanese amber of Early Cretaceous, and **Dominibythus inopinatus,** n. gen. n. sp., from Dominican amber of Late Eocene to Late Oligocene. The relationships of these tax to extant scolebythids are discussed.

The family Scolebythidae is a morphologically unusual and very rarely encountered group of chrysidoid wasps that has been only recently recognized (Evans 1963). The family may be immediately identified by its unique apomorphies that include a remarkably modified propectus. In the extant fauna, it is represented by three species, viz. *Clystopsenella longiventris* Kieffer, *Scolebythus madecassus* Evans, and *Ycaploca evansi* Nagy. The fossil *Cretabythus sibiricus* Evans was tentatively assigned to this family by Evans (1973), but is apparently not closely related to Scolebythidae (Rasnitsyn 1988). We describe below the first unquestionable fossil scolebythids, *Libanobythus milkii* gen. et sp. n. from Lebanese amber of Early Cretaceous age (135–120 Ma) and *Dominibythus inopinatus* gen. et sp. n. from Dominican amber of Late Eocene to Late Oligocene age (40–15 Ma). Considering the rarity of the family today, its occurrence in both ambers is noteworthy, particularly its presence in the Early Cretaceous.

Materials and Methods

Morphological terms used here are those in general use in aculeate systematics (e.g. Michener 1944, Richards 1977). The terminology and modified drawing conventions of Mason (1986) for stages of venational reduction are used. For brevity, the seven metasomal tergites and eight sternites are referred to as TI–TVII and SI–SVIII, respectively. All illustrations, except those of the male genitalia, were made with a camera lucida from specimens submerged in safflower oil to minimise optical distortion. The male genitalia of *Dominibythus inopinatus* were illustrated with an ocular grid at 160× magnification. The illustrations were refined using the Adobe Illustrator computer program (Adobe Systems Inc.).

The piece of Lebanese amber containing the holotype of *Libanobythus milkii,* like most Lebanese amber, was very fragile and contained many internal fractures before preparation. To strengthen the amber for polishing and to improve the clarity of the piece, the specimen was embedded in Ward's bioplastic. After embedding, the piece was polished down by hand as nearly as possible to the level of the fossil to improve the visibility of the wasp. The piece was then re-embedded in plastic to cover exposed portions of amber. Because of the clarity of the Dominican amber containing the holotype of *D. inopinatus,* this speci-

men was not embedded in plastic for study. [For permanent preservation of amber fossils, however, it is recommended that they be mounted in some type of clear medium to protect them from eventual oxidation that would otherwise tend to cause discoloration and cracking (Poinar 1992).] After polishing, the pieces were studied in safflower oil.

Age of the Fossils

The Lebanese amber specimen of *L. milkii* came from beds located near the mountainous villages of Jezzine and Dar al-Baidha. These beds occur in primary deposits of the Neocomian Epoch of the Early Cretaceous as well as in secondary deposits of the Barremian and Aptian stages. These deposits are dated from 120 to 135 million years old (Schlee and Dietrich 1970, Schlee and Glockner 1978).

The Dominican amber specimen of *D. inopinatus* originated from mines located in the Cordillera Septentrional, between Santiago and Puerto Plata, in the Northern Portion of the Dominican Republic. These mines are in the Altamira facies of the El Mamey Formation (Upper Eocene), which is shale sandstone interspersed with a conglomerate of well rounded pebbles (Eberle et al. 1980). Amber from these mines have been estimated by Lambert et al. (1985) to range from 15 to 40 million years old.

Characters of the Family

The fossils may be recognized as Scolebythidae by their enlarged and exposed diamond-shaped prosternum and posteriorly produced fore coxae bearing the fore trochanters laterally (Figs. 3, 6). These propectal characters are unique apomorphies of Scolebythidae (Brothers 1975, Carpenter 1986) and provide the strongest evidence for the family-group identities of the fossils. Both species also have most other apomorphies of the family listed by Brothers (1975) including a small, transverse clypeus, reduced metanotum (only visible in *D. inopinatus*), enlarged femora, and a complete lack of middle tibial spines. They also possess short, broad mandibles and venation that may be readily derived from the typical scolebythid pattern (Figs. 5, 7). Like extant scolebythids, both fossil forms have a convex and smoothly rounded first metasomal sternite that does not form an articulation with the second metasomal sternite and have a noticeably concave anterior surface on the first metasomal tergite. Like extant female scolebythids, the female of *L. milkii* possesses enlarged genae. Loss of the pronotal collar, which is another apomorphy of the family listed both by Brothers (1975) and Carpenter (1986), is present in *D. inopinatus* but not *L. milkii,* which has a less declivous and more elongate pronotum. Given this list of features, there can be no other taxonomic placement for the fossils.

As members of Chrysidoidea, the fossils possess the standard features of the superfamily including reduced forewing venation, lack of any closed cells in the hind wing (true of all Chrysidoidea except Plumariidae), 13-segmented female antennae and no jugal lobe.

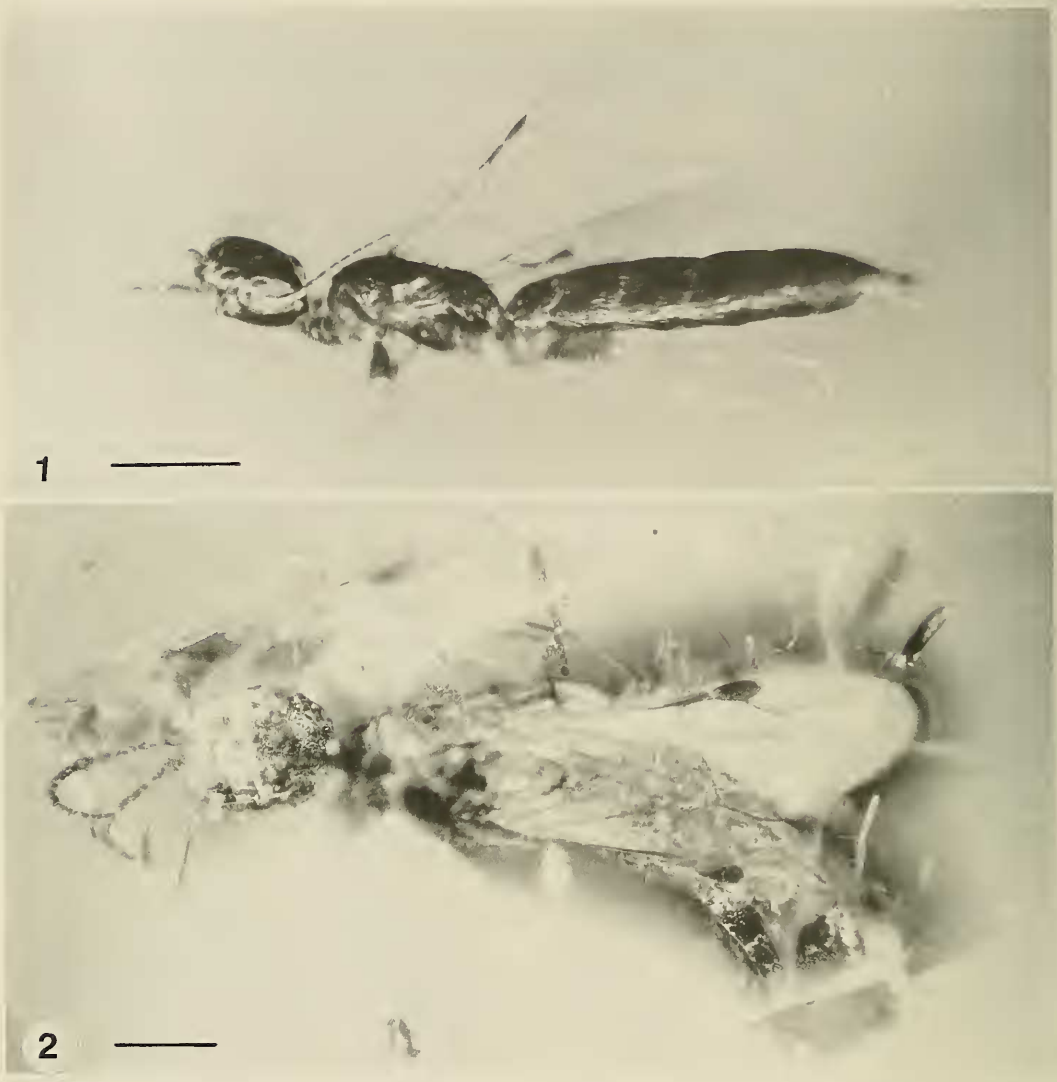
Key to Scolebythid Genera

1. R1 vein of forewing complete and fusing with Rs vein apically . . . . . extant genera, see Nagy (1975) for key
– R1 vein of forewing absent, not fusing with Rs vein apically (Figs. 5, 7) . . . . . extinct genera, 2
2. Discoidal cell defined by tubular veins, pronotum longer than scutum dorsally (Fig. 5) . . . . . *Libanobythus,* new genus
– Discoidal cell absent (Fig. 7), pronotum markedly shorter than scutum dorsally (Fig. 4) . . . . . *Dominibythus,* new genus

Dominibythus Prentice and Poinar, new genus

Type and only known species: *Dominibythus inopinatus,* new species.

Generic characters.—Frons elevated between antennal sockets, with carina arising at medial margin of antennal socket and extending outward dorsally creating two slightly depressed lateral areas that receive antennal scapes (Fig. 8). Orbits converging ventrally (Fig. 8). Ocelli positioned slightly



Figs. 1–2. 1, *Dominibythus inopinatus,* lateral view of left side. 2, *Libanobythus milkii,* dorsal view. Bars = 0.5 mm.

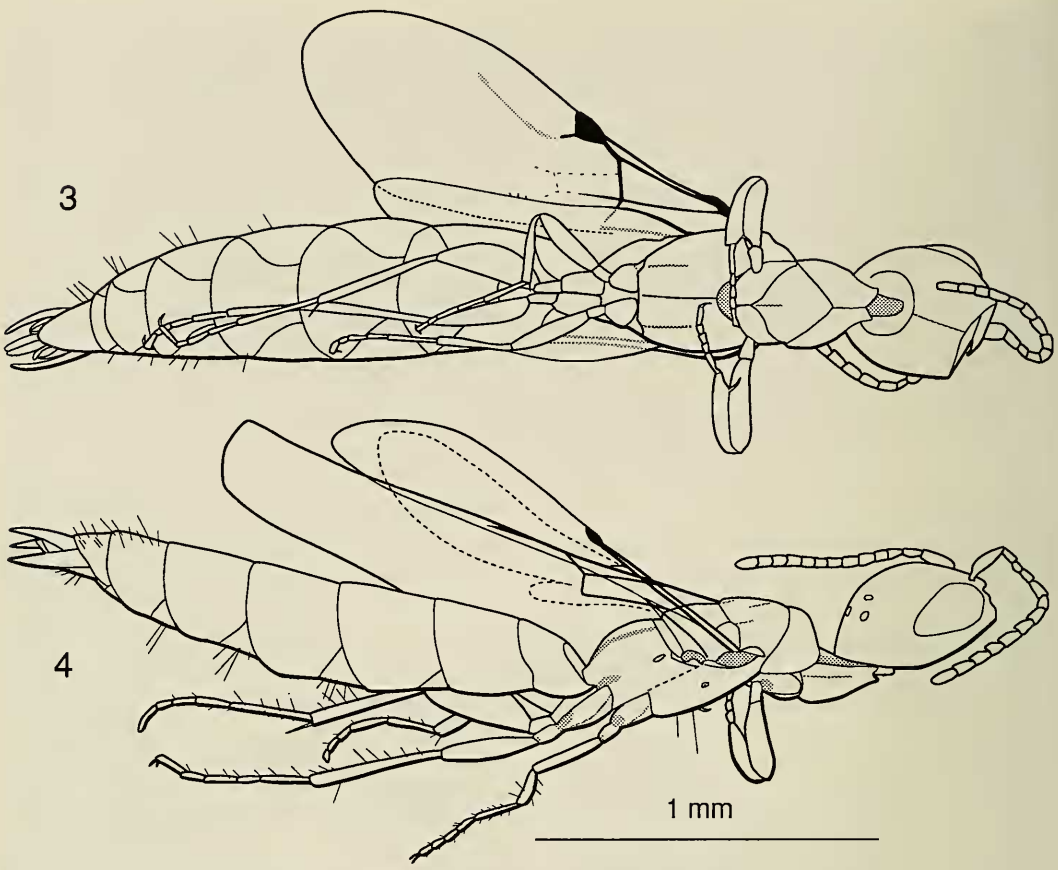
anterad of imaginary line connecting postero-dorsal margin of eyes. Clypeus conspicuously transverse, produced ventrally into a lobe that is about as wide as distance between outer margins of antennal sockets. Length of malar space equal to 0.5× basal mandibular width. Occipital carina present, at least ventrally, with gular sulcus extending along midline. Antenna arising very low on face, 13-segmented. Pronotum dorsally short, its length 0.2× length of mesoscutum, sharply declivous anteriorly; posterolateral lobes extending to tegulae. Propleuron well developed, anteriorly forming a neck separating head from pronotum, exposed dorsally. Prosternum large, diamond-shaped. Parapsidal lines long, positioned near lateral margins of mesoscutum. Notauli present only anteriorly. Mesoscutellum produced posteriorly as narrow rim overlying anterior margin of metanotum. Mesopleural signa comparatively long, extend-

ing from very near posterior margin of mesopleura half the distance to the antero-ventral margin of the mesopleura. Scrobe present and well-developed. Mesosternum simple, not produced as lamella over coxa. Metanotum short, its length 0.25× length of mesoscutellum. Propodeum with median longitudinal depression extending from anterior margin to near posterior rim, without evident metapostnotum dorsally. Tibial spur formula 1-1-1. Tarsal claws simple. Fore wing venation with R1 completely lacking; Rs+M as spectral vein; apical portion of Rs represented by an exceedingly light nebulous vein; first free abscissa of Cu nebulous, apically becoming spectral (Fig. 7); stigma conspicuous, slightly convex on costal margin. Hind wing venation reduced to costal vein extending 0.3× length of wing and to very base of anal vein. Jugal lobe absent. Metasoma with no constriction between first and second segments. Metasomal tergites dorsally comparatively flat in cross-section, sternites somewhat convex in cross-section; male with seven exposed tergites and eight exposed sternites. First metasomal tergite with a well formed depression on the anterior face fitting the posterior portion of the propodeum. First metasomal sternite evenly convex apically, not forming an articulation with SII.

Derivation of name.—The name *Dominibythus* is a combination of Dominican (referring to the Dominican Republic) and Scolebythus.

Dominibythus inopinatus Prentice and Poinar, new species (Figs. 1, 3, 4, 7–9)

Male.—Length 2.8 mm. Color: Head, mesosoma and metasoma brown; legs, antennae, mouthparts and genitalia tan; wings clear, veins tan. Sculpture and vestiture: Head smooth, with microscopic punctures that are about 2 ocellar diameters apart, with no visible vestiture; mesosomal cuticle microscopically areolate, with a few erect setae on venter; metasoma with some sparse, erect setae, 1–2 mid antennal flagellomeres in length; most metasomal setae on more apical segments. Fore, mid, and especially hindtibiae bearing setae whose length nearly averages that of tarsomere II. Fore and hind wing bearing minute, evenly spaced setae on apical half. Structure: Head 0.45 mm from vertex to ventral margin of clypeus and 0.45 mm in maximal width. Frontal line present, extending from near anterior ocellus to between antennal sockets. Ocellar triangle slightly elevated; ocello-ocular distance slightly greater than width of ocellar triangle; distance between lateral ocelli 1.5× diameter of a lateral ocellus. Width of gena 0.5× width of eye in lateral view. Proboscidial fossa short and wide, width 6× length. Occipital carina separated from proboscidial fossa by approximately the length of 4 mid-flagellomeres. Scape somewhat flattened in cross-section, length, including radicle, approximately 2× greatest width. Length of pedicel 2× length of first flagellomere, slightly less than length of scape without radicle; length of flagellomere II approximately 1.5× length of flagellomere I; flagellomeres III–X approximately equivalent in length and slightly longer than flagellomere II; length of flagellomere XI 1.3× length of flagellomere X. Mandibles relatively short, subapical teeth not visible although ventral one well produced apically. Mesosoma 0.9 mm in length. Mesoscutum about as long as mesoscutellum; median longitudinal impression evident. Epicnemial sulcus apparently present below pronotal lobe and extending ventrally to midline near very anterior margin of mesopleura. Propodeal spiracle with well-developed operculum and placed very near propodeal anterior margin, completely on lateral propodeal face. Fore femur robust, length slightly less than 3× width, widest distally; length of hindfemur slightly more than 3× width. Fore tibia about as long as fore femur; mid and hind tibiae slightly longer than respective femora. Length of hindtibial spur about 0.5× length of hindbasitarsus. Fore tarsus about as long as fore tibia; mid and hind tarsi longer than



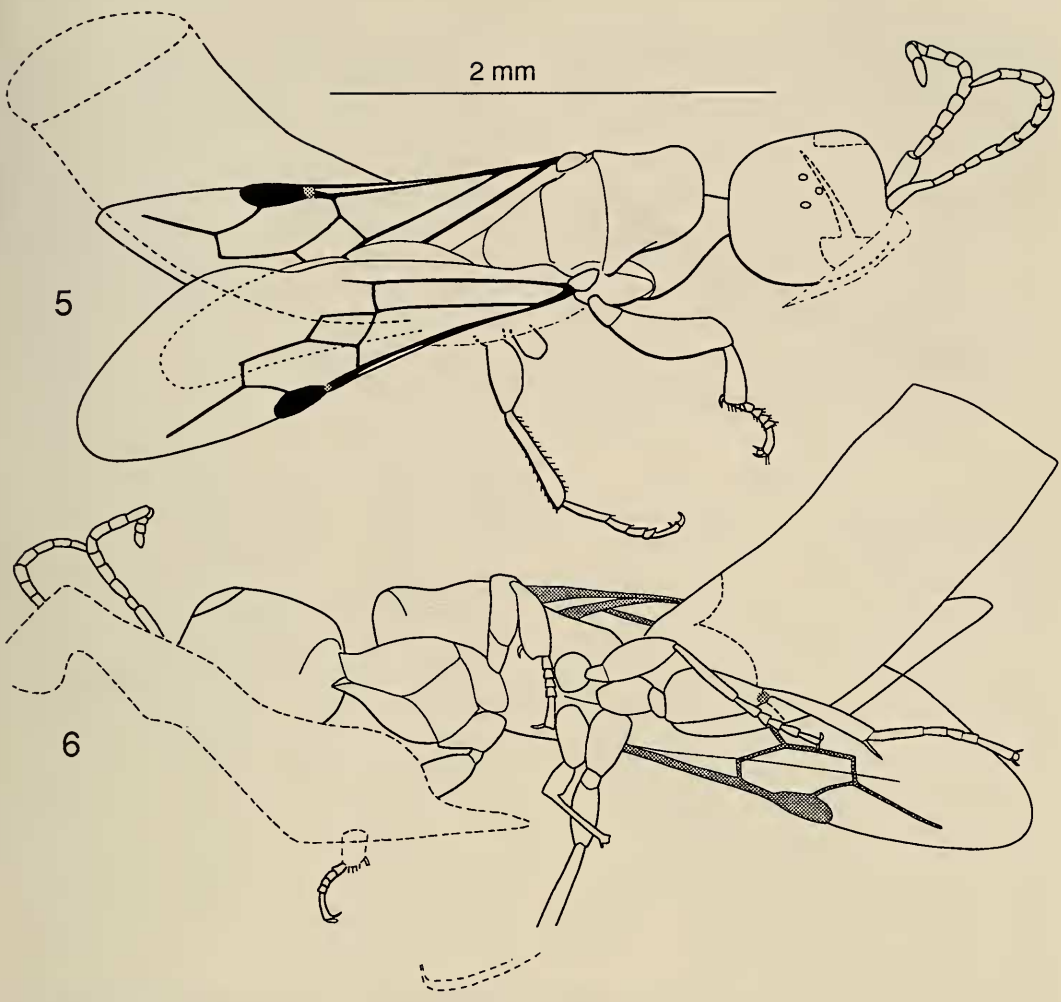
Figs. 3–4. *Dominibythus inopinatus.* 3, Ventral view. 4, Dorsolateral view.

their respective tibiae. Fore wing 1.4 mm in length; costal vein bearing a number of relatively well-developed setae that form a fringe approximately as wide as the prestigma. Hind wing with three hamuli; length of vannal lobe approximately 0.3× length of hind wing; posterior margin of hind wing bearing a fringe of well-developed setae that is as wide as the fringe on the costal margin of the fore wing. Metasoma elongate, 1.6 mm long (excluding genitalia). Length of second metasomal tergite approximately 1.3× length of TI. Length of first metasomal sernite about 1.5× length of TI. Subgenital plate clearly exposed and entirely convex on apical margin (Fig. 9). Aedeagus extending slightly beyond imaginary line drawn between apices of gonapophyses; gonapophyses bearing at least a few, very fine setae apically (Fig. 9); gonapophyseal setae about equivalent to width of gonapophyses near tip in length. The male genitalia of the holotype are exposed. In the normal position they would be concealed by TVII and SVIII.

Female.—Unknown.

Derivation of name.—The Latin *inopinatus,* meaning unexpected, refers to the seemingly improbable discovery of this wasp in Dominican amber given the rarity of the family in the extant fauna.

Material examined.—Holotype ♂: a superbly preserved wasp in Dominican amber with locality data as described under Age of the Fossils. It is in a clear piece of amber approximately 7 mm in length (specimen #7594, Smithsonian Dominican amber Brodzinsky/Lopez-Penha collection).

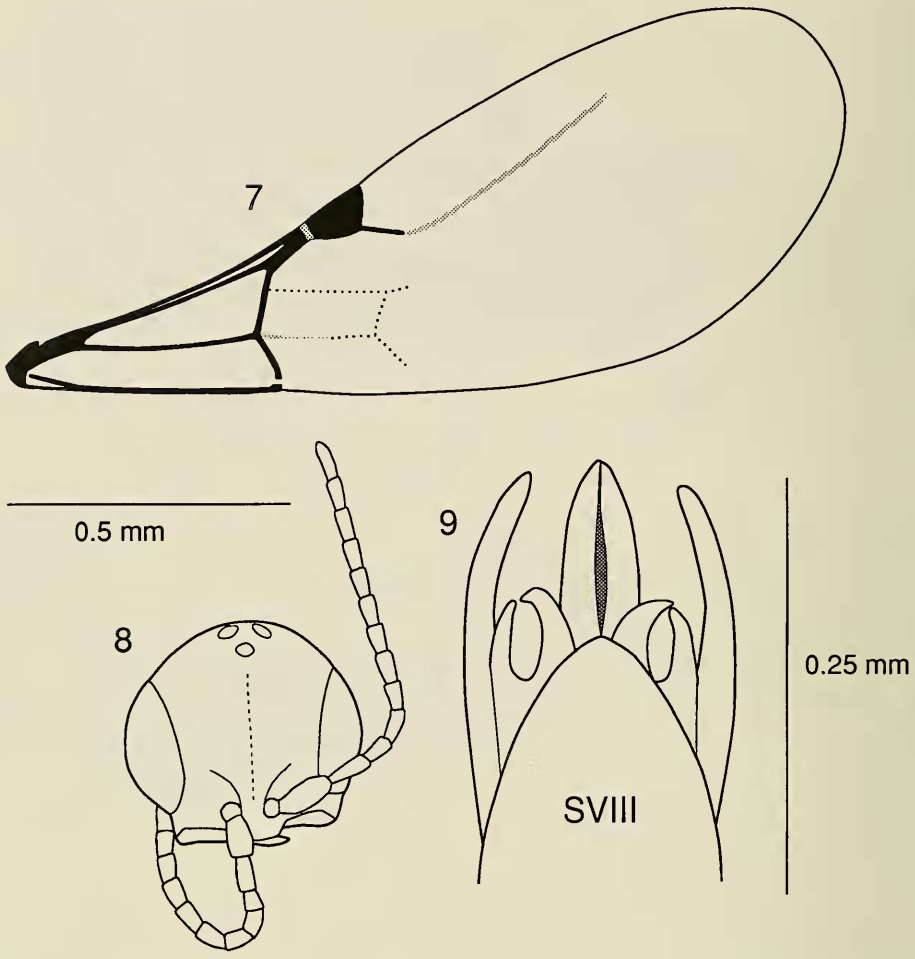


Figs. 5–6. *Libanobythus milkii.* 5, Dorsal view. 6, Ventral view.

Libanobythus Prentice and Poinar, new genus

Type and only known species: *Libanobythus milkii,* new species.

Generic characters.—Frons not elevated between antennal sockets with no evident carinae. Inner orbits evenly convex, closest near middle. Lateral ocelli positioned slightly posterad of imaginary line connecting postero-dorsal margin of compound eyes. Clypeus very short, transverse. Gena well developed, wider than eyes in lateral view. Occipital carina present, at least ventrally. Antennae placed very low on face, 13-segmented. Mandibles short, broad. Maxillary and labial palpi apparently 4-segmented. Pronotum nearly 1.5× as long as mesoscutum, not sharply declivous anteriorly; postero-lateral lobe of pronotum extending to tegula. Propleura well developed, anteriorly forming a neck that separates head from pronotum. Prosternum exposed and diamond-shaped. Parapsidal lines and notauli apparently absent. Mesosternum simple, not produced as lamellae over mid coxa. Tibial spur formula apparently 1-1-1. Tarsal claws simple. Forewing with vein R1 completely lacking; vein Cu absent beyond 1m-cu cross-vein; apical abscissa of anal vein slightly longer than cross-vein cu-a;



Figs. 7–9. *Dominibythus inopinatus*. 7, Right forewing, nebulous veins indicated by stiplings, spectral veins indicated by dotting. 8, Face. 9, Male genitalia, ventral aspect with outline of last sternum indicated.

apical portion of vein Rs extending close to costal margin, its length 3× length of crossvein 2r-rs, tubular throughout; stigma slightly convex on costal margin (Fig. 5). Hind wing vannal lobe extending 0.4× length of hindwing; jugal lobe absent. No constriction between first and second metasomal segments; segments wider than high. First metasomal tergite with depression fitting end of propodeum. First metasomal sternite evenly convex apically, not forming articulation with SII.

Derivation of name.—*Libanobythus* is a combination of the names Lebanon and Scolebythus and is in reference to the country of origin of the fossil.

Libanobythus milkii Prentice and Poinar, new species

(Figs. 2, 5, 6)

Female.—Body length approximately 4 mm not including apical metasomal segments which are missing from holotype. Color: Head, mesosoma and metasoma piceous; legs, antennae and mouthparts brown; wings clear, radial vein and stigma brown, other veins brownish-yellow. Sculpture and vestiture: Head smooth, with at least a few short, erect setae on genae. Pronotum and mesonotum smooth; pronotum bearing some erect setae approximately 0.05 mm in length. Metasoma bearing nu-

merous scattered setae, at least ventrally, approximately 0.1 mm in length. Legs with numerous scattered setae from 0.05 to 0.1 mm in length, best developed on mid and hind tibiae. Wings without evident setae. Hindwing bearing a fringe of setae approximately 0.02 mm in width. Fringe of same width extending from fore wing costal vein. Structure: Head 0.65 mm wide, 0.75 mm from vertex to ventral margin of clypeus. Width of ocellar triangle about equal to ocello-ocular distance; distance between lateral ocelli about 2.5× diameter of a lateral ocellus. Scape flattened, length including radicle, approximately 2.5× greatest width. Pedicel moderately long, its length 2× length of first flagellomere. Flagellomeres II–X nearly equal in length, approximately twice as long as flagellomere I; length of flagellomere XI 1.5× length of flagellomere X. Mesosoma, including propleura, approximately 1.4 mm in length. Pronotum subequal to mesoscutum in length. Fore femur robust, 2.4× as long as wide; mid femur robust, length slightly more than 2× width; hind femur very robust, length slightly less than twice greatest width. Fore tibia slightly shorter than fore femur; mid and hind tibiae approximately equal to respective femora in length. Length of hind tibial spur less than 0.5× length of hind basitarsus. Fore tarsus shorter than fore tibia; mid and hind tarsi longer than their respective tibiae. Fore wing 2.4 mm in length. Hind wing with four hamuli. Length of vannal lobe slightly less than 0.4× total hind wing length.

Male.—Unknown.

Derivation of name.—This species is named for Dr. Raif Milki.

Material examined.—Holotype ♀: a not well preserved specimen of an almost entire wasp from Lebanese amber with locality data as described under Age of the Fossils. The fossil is covered with numerous small air bubbles and cracks that obscure many details. The wasp is also lacking the last few metasomal segments. It is embedded in a piece of plastic measuring 1 cm × 1 cm × 0.5 cm. The specimen is part of Dr. Raif Milki's Lebanese amber collection maintained at the American University of Beirut.

Preservation.—The specimen lacks the end of the metasoma, but may be identified as a female due to its overall robust form, powerfully built legs (particularly the fore femora) and enlarged genae. Male scolebythids are more delicately built, with slenderer legs and less well developed genae. Because of the state of preservation of this wasp, its description is not entirely comparable with that of *D. inopinatus*.

Relationships

The elongate pronotum that retains a pronotal collar in *Libanobythus milkii* suggests a sister-group relationship between this species and other known Scolebythidae since the loss of the collar in other scolebythids is very likely derived within Chrysidoidea (Brothers 1975, Carpenter 1986). This sister-group relationship would not be unexpected given the age of the fossil, but, if true, means the complete absence of vein R1 in both *L. milkii* and *D. inopinatus* is convergent. The elongate pronotum and presence of a pronotal collar in *L. milkii* provides further support for the views of Brothers (1975) and Carpenter (1986) whose cladistic analyses indicated that the loss of the pronotal collar in Plumariidae (most probably the sister-group to other Chrysidoidea (Brothers 1975, Carpenter 1986)) and Scolebythidae is convergent. The alternative, that the absence of the collar in Plumariidae and some scolebythids is homologous and thus a groundplan feature of Chrysidoidea, as Koenigsmann (1978) believed, is now especially unlikely.

Dominibythus inopinatus appears to be most closely related to *Ycaploca evansi* as indicated by the presence in both taxa of a frontal prominence between the antennae that is marked laterally by two dorsally diverging carinae (Fig. 8). This feature is not evident in any of the other species of Scolebythidae. *Dominibythus inopinatus* also shares a well developed clypeal lobe, pro-

podeal groove and evenly convex subgenital plate with *Ycaploca,* but these features are also present in *Scolebythus.* An apparent tibial spur formula of 1-1-1 may be an additional character linking *D. inopinatus* with *Y. evansi* since *Scolebythus* and *Clystopsenella* have the ancestral tibial spur formula of 1-2-2. *Dominibythus inopinatus* may be distinguished from *Y. evansi,* and other extant scolebythids, by its much more reduced wing venation which does not include a complete marginal, submarginal or discoidal cell, by its more strongly diverging frontal carinae, by its lack of well developed notauli and by its lack of an evident metapostnotum on the propodeum.

Discussion

The addition of two new monotypic fossil scolebythid genera to the three extant monotypic genera might seem to unnecessarily clutter this small family with genera. However, on phenetic grounds, the recognition of five genera is justified. Neither fossil species may be placed in a currently defined genus and both are as morphologically distinct as any of their extant relatives. This taxonomic arrangement simply reflects the relictual status of this group and accords with the great range in age of the included species. Unfortunately, this scheme does not represent any cladistic or phenetic relationship between the species.

When Evans (1963) described the family, he speculated that the species attacked wood-boring beetle larvae based on their possession of some characteristics reminiscent of wasps, such as Aulacidae, having such a biology. Features mentioned by Evans (1963: 14) are "the broad mouth opening and powerful mandibles, the reduced clypeus, and the strong malar space; on the thorax the elongate proepisterna, perhaps the large prosternum, and the flattened coxae." Evans (1963: 8) also identified a well developed proepimeron in scolebythids that he stated as ". . . completely set off by sutures from the proepisterna." From studying his figures and specimens of *Clystopsenella longiventris* and *Ycaploca evansi,* as well as the fossil material, however, it appears that this "so-called" proepimeron is actually a part of the fore coxa that extends as a lobe basad of the insertion of the trochanter. Based on collection data from a number of specimens of *Y. evansi,* Nagy (1975) and Brothers (1981) have essentially confirmed Evans' (1963) original speculation. The information indicates that scolebythids develop on wood-boring beetle larvae (Cerambycidae) that are attacked in their host beetle's burrows. Of interest is the possibility that they are gregarious parasitoids (Brothers 1981), which, if true, is unusual for an aculeate. Given the nearly identical modifications of the fossil scolebythids to their extant relatives, it is very likely that they, too, attacked wood boring beetle larvae in the same manner as living scolebythids.

In addition to the features listed by Evans, other peculiar apomorphies of the family include the convexity of SI, the lack of an articulation between SI and SII, the deep concavity in TI that fits the end of the propodeum, the transverse flatness of the tergites as opposed to the convexity of the sternites, and the overall length of the metasoma. Possibly these features facilitate movement through their host's burrows, although it is curious that each modification would seem to allow the metasoma to be more freely articulated dorsad. Possibly this is an alternative means for bringing the sting to bear on the prey; if true, this would differ from the movement of other aculeate wasps which universally articulate the metasoma downward and below the body for stinging prey. If anything, the peculiar modifications of the propectus enhance this idea, for the form of the propectus allows the head to be strongly directed dorsad (as seen in the fossils and pinned scolebythids), and the fore legs to be brought forward; this could allow the mandibles and forelegs to grip the prey while stinging with the metasoma held up and over the body of the wasp.

By attacking wood boring beetle larvae, scolebythids are exposed to places (such as the bases of resin producing trees) where they may be trapped in resin having the possibility of subsequent fossilization. Thus, like many other aculeate wasp taxa that have been found in amber, the biology of scolebythids increases the probability that they may be found in amber. This may partially explain their occurrence in both Lebanese and Dominican ambers, although it is also possible that the family may have been more common in the geologic past.

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